

(Cramp & Simmons 1977: 135), the record is certainly no more extraordinary than that from Lisianski, where human interference was never regarded as a possibility, particularly given the natural propensity for petrels to wander far out of their normal ranges (Bourne 1967). Considering that the Italian bird was accompanied by 2 others like it and came to land during a period of storm, I see no reason to question the naturalness of this occurrence. I would regard transportation of 3 of these birds to the Mediterranean by a sailor to be far more unlikely than their having arrived on their own; the possibility that they may have come from some population other than those in the western Indian Ocean, a possibility which is supported by the differences in foot colour, further supports the validity of the Italian record.

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## Systematics of the *Turdus fumigatus/hauxwelli* group of thrushes

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There has been much disagreement about the systematic treatment of the thrushes for which the specific names *fumigatus*, *hauxwelli* and *obsoletus* are used. The group is widely distributed, from Costa Rica and Panama through much of northern South America south to Bolivia, Mato Grosso and southeastern Brazil (Fig. 1). They are lowland forest thrushes, brown above and paler and more rufous below, mostly with dark bills, and without a coloured eye-ring. Part of the difficulty is the usual one affecting groups of closely related forms with geographically isolated populations: whether to treat moderately differentiated allopatric forms as specifically or only subspecifically distinct. A further difficulty,

however, arises, from the fact that in parts of central Amazonia there are variable populations that may be broadly divided into 2 colour types (*fumigatus* and *hauxwelli*), and there has been uncertainty as to whether 2 species coexist in this area, as Gyldenstolpe (1945) concluded, or whether there is a variable population resulting, perhaps, from secondary contact between 2 distinct but still conspecific forms.

The main purpose of this paper is to examine, in more detail than has been done heretofore, the situation in central Amazonia, and to suggest the systematic treatment that is most consistent with the known facts. The recent distributional history of this group of thrushes is also briefly discussed.

I have had for examination what are still, it seems, the 2 best series available of thrushes of the *fumigatus/hauxwelli* complex from central and upper Amazonia and adjacent parts of Bolivia: 39 specimens from the Carnegie Museum, and 28 specimens from the Stockholm Museum. It was as a result of studying the Stockholm series that Gyldenstolpe came to the conclusion mentioned above.

### Distribution and geographical variation – the general picture

Figure 1 shows the greater part of the known distribution of the group under consideration. The following are the salient points relevant to the present discussion.



Fig. 1. Map of Brazil and adjacent countries showing the distribution of *Turdus fumigatus* in Central and South America (except for part of eastern Brazil). Populations are probably continuous across Amazonia from the west (*T.f. hauxwelli*, *ha* on map) to the east and northeast (*T.f. fumigatus*, *fu* on map), as indicated by the stippling and the unstippled central area containing the named rivers and 9 plumage scores — see text. Question marks north of this area indicate areas where the species is still unknown. Other subspecies as follows: *or*, *orinocensis*, known from 3 disjunct areas; *aq*, *aquilónalis*, also from 3 disjunct areas (presumably intergrading with *fumigatus* to the southeast); *co*, *colombianus*; *pa*, *parambanus*; *ob*, *obsoletus*.

The whole of the eastern and northeastern parts of the range is occupied by birds with warm brown upperparts (Ridgway's *antique-brown/raw umber*, the oblique stroke indicating a tint intermediate between the two named) and paler, warm rufous brown underparts (Ridgway's *cinnamon/clay*, verging to bright *antique-brown*). There is no, or only a very small, white belly patch; the under tail-coverts are bright cinnamon; and the bill is blackish. There are other differences in particular parts of the plumage from the form that occurs in western Amazonia, but they are all, it seems, basically consequences of the brighter, more rufous plumage coloration. These rufous birds are divided into 4 slightly differentiated subspecies: *fumigatus* in eastern Brazil, the Guianas and eastern Venezuela; *aquilonalis* along the coast of northern Venezuela and in Trinidad; and 2 outlying Antillean populations, *personus* in Grenada and *bondi* in St. Vincent. The east Brazilian coastal population is isolated from the populations to the west, and it seems that the birds are sparsely or patchily distributed in a vast area south of the Amazon; at any rate there are few records.

Upper Amazonia, from Bolivia in the south probably to southern Colombia in the north, is occupied by birds with less warm brown upperparts (Ridgway's *cinnamon brown* with olive wash) and markedly duller brown underparts (Ridgway's *clay colour/drab*). There is a pure white belly patch extending forward to about the middle of the folded wing; the under tail-coverts are mainly white with fawn-brown edges; and the bill tends to have a yellowish tip (greenish or brownish in dried skins). These are the birds to which the name *hauxwelli* is applied (type locality: Pebas, on the Peruvian Amazon). To the north, the populations of the upper Orinoco and the eastern base of the Andes in Colombia and western Venezuela (*orinocensis*) are intermediate between *hauxwelli* and *fumigatus* in colouring. They have been linked with both, i.e. treated as a subspecies of *fumigatus* (e.g. Zimmer & Phelps 1955) or of *obsoletus* = *hauxwelli* (e.g. Meyer de Schauensee & Phelps 1978). (In Peters' *Checklist* (Ripley 1964) the Orinoco region of southern Venezuela is listed in the range of both *T.f. orinocensis* and *T.b. hauxwelli*, apparently through misinterpretation of earlier literature, in which the original specimen, from Nericagua on the upper Orinoco, was first treated as *hauxwelli* and later as a subspecies of *fumigatus*.)

The intermediate character of *orinocensis* suggests that it may be linked both to *hauxwelli* populations to the south and to *fumigatus* populations to the east (Fig. 1); but there is a gap in the known range in southern Venezuela, between the Orinoco and the Rio Paragua where *fumigatus* is recorded. It seems unlikely that there are no populations of this group of thrushes in the intervening 500 km gap.

Naumburg (1930) reported that birds from western Mato Grosso are also intermediate between *fumigatus* and *hauxwelli*. Few specimens have been collected in southern Amazonia, between Bolivia and the Belém area, but here, as in southern Venezuela, it may be suspected that there is a transition from *hauxwelli*-type to *fumigatus*-type populations.

Between these 2 possible transition zones, about which little is known, lies the area where Gyldenstolpe (1945) reported that birds of *hauxwelli* type coexist with birds of *fumigatus* type.

Finally, west of the Andes there are 3 populations: *obsoletus* in Costa Rica, Panama and extreme northwest Colombia; the closely related *parambanus* along the Pacific slopes of the Western Andes of Colombia and Ecuador; and, slightly more distinct, *colombianus* in a limited area on the east slopes of the Western Andes in the Cauca and Patía valleys. Their taxonomic treatment has been varied.



Hartert (1920) was the first to suggest that they should all be treated, as well as *hauxwelli*, as subspecies of *fumigatus*, and Hellmayr (1934) adopted this treatment; but many authors have maintained *obsoletus* as a separate species, in which *hauxwelli* may also be included (e.g. Ridgely 1976). Ripley (1964), who treats *fumigatus* and *hauxwelli* as specifically distinct, links *colombianus* with *hauxwelli*, presumably because it has distinctly olive-brown rather than rufous-brown upperparts, and *obsoletus* and *parambanus*, which have rufous-brown upperparts, with *fumigatus*. Slud's (1964) description of the calls of *obsoletus* in Costa Rica suggests that they are distinctly different from those of *fumigatus* in Trinidad (pers. obs.). Until a thorough study has been made of all aspects of the biology of these western forms it seems best to maintain a wide polytypic species concept and link them with the forms east of the Andes. They are not considered further here.

### The situation in upper Amazonia

As mentioned, from a study of specimens collected in central and upper Amazonia, especially on the rivers Purús and Juruá, Gyldenstolpe (1945) concluded that *fumigatus* and *hauxwelli* are distinct species, and that they overlap in this area. He admitted, however, that *hauxwelli* is variable, and in particular that birds from northern Bolivia tend towards *fumigatus*-type plumage (cf. Naumburg (1930) on birds from western Mato Grosso, adjacent to Bolivia, mentioned above); but he decided nevertheless that they "must be assigned to that species [*hauxwelli*] rather than to *T.f. fumigatus*". In reaching this decision, Gyldenstolpe was undoubtedly hampered by a typological mode of thinking that tended to force specimens into hard-and-fast taxonomic categories.

TABLE 1

Scoring of 10 plumage characters in the *Turdus fumigatus/hauxwelli* group of thrushes

	<i>fumigatus</i> type	<i>hauxwelli</i> type
1. General colour of upperparts	<i>antique brown/raw umber</i>	<i>cinnamon brown with olive brown wash</i>
2. General colour of underparts	<i>cinnamon/clay</i> , verging to bright <i>antique brown</i>	<i>clay colour/drab</i>
3. Belly patch	absent or very small	pure white, extending forward to about level of mid-wing
4. Under tail-coverts	bright <i>cinnamon</i>	mainly white, dull brown (more or less <i>fawn</i> ) edges
5. Leg feathering	<i>clay colour</i>	<i>fawn/grey</i>
6. Inner webs of remiges	broad bright <i>cinnamon</i> edges	no cinnamon edges
7. Outer edges of remiges	<i>cinnamon/antique brown</i>	<i>clay colour</i>
8. Under wing coverts	bright rufous	dull rufous
9. Upper surface of tail	with rufous sheen	with blue-purple sheen
10. Rump	bright, approaching <i>amber brown</i>	<i>cinnamon brown</i>

For each of the 10 characters, a score of 0 was given for *fumigatus* type, 4 for *hauxwelli* type, and 1, 2 or 3 for different degrees of intermediacy. Each specimen was then given a final score based on the mean of all 10 scores; thus a pure *fumigatus*-type bird scores 0.0 and a pure *hauxwelli*-type bird 4.0.

Italicised colours are from Ridgway (1912).

In an attempt at an objective analysis of the situation in upper Amazonia, I have classified each specimen on the basis of 10 plumage characters, each of which may be scored from 0 to 4, a score of 0 being assigned to *fumigatus*-type coloration and a score of 4 to *hauxwelli*-type coloration (Table 1). The mean of all 10 scores thus indicates to what extent an individual bird resembles one type or the other. Since the colour characters are not, and would not be expected to be, independent of one another there is a tendency for individuals to have similar scores for most of the characters; but this is by no means always the case. Thus some birds score 4 for most characters, but 0 for the belly patch. All that is claimed for this procedure is that it is more reliable than a judgment based on one or two characters only, or on a general impression.,

Two other characters, bill-colour and wing-tip shape, were considered but are not used in the analysis: (1) *The bill-colour* of the birds of *hauxwelli* type, as already mentioned, tends to be paler at the tip (appearing greenish or brownish in dry skins) than that of birds of *fumigatus* type (dark brown or blackish). The colour is, however, related to age, and may vary with season, and in any case is not always easy to judge. (2) *The wing-tip* shape may show some difference. Eisenmann (MS) noted that birds of *fumigatus*-type generally have the 2nd primary (from the outside) longer than the 7th in the folded wing; while birds of *hauxwelli* type have the 2nd primary either shorter than or of the same length as the 7th, which means that they have a more rounded wing. I have examined this character in a large number of specimens, from Amazonia and elsewhere, and also in other *Turdus* spp., and have had to exclude it from the analysis. In the first place, there is a definite tendency in *Turdus* for birds in first-year plumage (i.e. with their first set of flight-feathers) to have slightly more pointed wings than older birds. This may be related to the need for young birds to disperse, and so to have to fly farther and more often than adult birds. But in particular cases it is not always easy or even possible to distinguish birds in first-year plumage from older birds, especially when the plumage is worn. Secondly, even in birds of the same age-category, wing-tip shape is rather variable. Hence large samples are needed in order to detect slight differences in wing-shape between populations. Nevertheless, birds of *fumigatus* and *hauxwelli* types probably do differ slightly on average, as shown in Table 2.

No consistent differences were found in any other mensural character (wing-length, relative tail-length, culmen-length, tarsus-length) between birds of *fumigatus* and *hauxwelli* types.

TABLE 2  
Wing-tip shape of birds of *Turdus fumigatus*  
and *T. hauxwelli* plumage types

Length of 2nd primary (p2) in relation to inner primaries	<i>fumigatus</i> type (N = 32)	<i>hauxwelli</i> type (N = 42)
= p6	1	—
between p6 and p7	7	14
= p7	17	17
between p7 and p8	7	10
= p8	—	1

Notes. Primaries are numbered from the outside; Birds with longest p2 (= p6) have most pointed wings; those with shortest p2 (= p8) have most rounded wings; *fumigatus* type includes some specimens of the very similar subspecies *aquilonalis*, from Trinidad.

TABLE 3

Plumage scores (see Table 1) for 9 samples of birds from middle and upper Amazonia of the *Turdus fumigatus/hauxwelli* group of thrushes

		N	Scores	Mean score
Brazil	Lower Tapajós	8	0-1.5	0.4
	Lower Madeira	3	1.2-1.6	1.3
	North side of middle Amazon (Manacapuru and Codajaz)	5	0-0.9, 3.2	1.0
	Lower Purús	8	0.3, 0.8, 3.2-3.8	2.7
	Middle Purús	26	2.1-3.6	3.1
	Upper Amazon (Tonantins)	2	3.4, 3.4	3.4
	Juruá	6	3.3-3.6	3.5
Peru	Loreto	3	3.0-4.0	3.4
Bolivia	El Beni and Santa Cruz	6	2.4-3.1	2.7

Table 3 shows the scores for 9 samples from the area between the upper Amazon in Peru, Bolivia and the Rio Tapajós in middle Amazonia; the mean scores are also shown in Fig. 1. It is evident that birds from the lower Tapajós are pure, or almost pure, *fumigatus* type. Populations from Amazonian Peru, the upper Amazon in Brazil, the Juruá and the upper and middle Purús, with mean scores of 3.1-3.5, are predominantly of *hauxwelli* type. The mean score for Bolivian birds (2.7) confirms Gyldenstolpe's statement, that they tend slightly towards *fumigatus* type. Populations from the lower Madeira, from north of the middle Amazon (Codajás, Manacapuru) and from the lower Purús are intermediate, with mean scores of 1.0-2.7.

TABLE 4

Individual scores (see Table 1) for middle and upper Amazonian samples of the *Turdus fumigatus/hauxwelli* group of thrushes

Score	total	N	intermediate populations*	Score	total	N	intermediate populations
3.8-4.0	2		1	1.8-1.9	—		
3.6-3.7	3			1.6-1.7	1		1
3.4-3.5	12		2	1.4-1.5	1		
3.2-3.3	11		4	1.2-1.3	2		2
3.0-3.1	9			1.0-1.1	—		
2.8-2.9	5			0.8-0.9	2		2
2.6-2.7	4			0.6-0.7	1		
2.4-2.5	3			0.4-0.5	2		2
2.2-2.3	—			0.2-0.3	1		1
2.0-2.1	1			0.0-0.1	7		1

\*Lower Madeira, Codajás and Manacapuru, lower Purús.

Table 4 shows the distribution of individual scores for the whole sample combined, and also for the specimens from the 3 intermediate areas mentioned above. It is apparent that the scores cover almost the whole of the possible range, but there are few around the middle of the range. This is evident also for the sample from the area of intermediacy. It seems that there is both intergradation between the two types, and also a tendency for them to maintain their identities.

## Discussion

The situation revealed by the analysis may be interpreted in more than one way. It seems most likely that it is the result of secondary contact between two populations, *hauxwelli* in the west and *fumigatus* in the east, and that the contact is fairly recent. It does not seem possible that the distribution of scores as shown in Table 4 could be produced unless individuals of either type tend to mate with birds of their own type. Possibly this tendency is reinforced by, or even solely due to, a tendency to prefer different habitats. If this is so, one may guess that *hauxwelli*-type birds prefer heavy primary forest and *fumigatus*-type birds lighter, more open forest. This would be in accordance both with prevailing forest types in their putative areas of origin (upper Amazonia with humid forest, eastern regions with more seasonal forests) and with the slight difference in wing-shape, a rounded wing-tip being associated with dense forest habitat and a more pointed wing with more open habitat in the genus as a whole.

With the data available this can be no more than a suggestion for future investigation. It would be especially desirable to carry out detailed field work in the area where both types occur, and to score the plumage and other characters of birds trapped in different kinds of forest and of known pairs. Vocalisations should also be studied, in particular alarm calls, which are probably less variable than songs and show marked interspecific differences in other groups of *Turdus* species.

As regards formal taxonomic treatment, the fact that *hauxwelli* appears to intergrade with *fumigatus*-type populations in the Mato Grosso area of Brazil and the upper Orinoco area, and that in the part of central Amazonia under consideration here individuals of all degrees of intermediacy occur (even though there is a distinctly bimodal distribution), indicates that the only practical course is to treat all populations as conspecific, at least pending further study. If this is done, there is every reason to include the very similar populations west of the Andes, again provisionally and pending further study.

Any attempt to reconstruct the distributional history of this group of forms must be highly speculative. Following Haffer (1974) one might suggest that *fumigatus* differentiated in a forest refuge in the east; but on the basis of present distribution it might be the Guianan, the Belém, or even the southeastern Brazilian refuge. The Guianan refuge is perhaps the least likely, since from this refuge one would expect populations to have spread further west in Venezuela than they have done. *hauxwelli* may have differentiated in an upper Amazonian refuge. It is unlikely that it can have recently spread into upper Amazonia from the trans-Andean forests where birds of similar type now occur, since the species is absent from the 2 areas which provide the easiest access from trans-Andean to Amazonian lowland forest, namely the lower Cauca and Magdalena valleys in the north and the low Andean passes in extreme northwest Peru.

It is unprofitable to speculate further on the distribution history of a single species such as this without taking into account other species with similar overall distribution patterns. For instance, a number of forest species extend along the Caribbean coast of Central America as far as western Costa Rica, as *T. fumigatus* does, and one would like to know whether this indicates a relatively recent extension into Central America and is associated with particular distributional patterns in South America. Similarly, several other species have similar populations in eastern Amazonia and (now isolated) in southeastern Brazil, and distinct populations in western Amazonia. It will also be necessary in attempting any



historical reconstruction to take into account present constraints on distribution, which may not be obvious without detailed ecological study. A case in point is the apparent absence of *Turdus fumigatus* from the upper half of the Rio Negro. Possibly this has an explanation in the relative poverty of the forests along this black-water river (Janzen 1974), which may produce relatively poor feeding conditions for species that forage on the forest floor.

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## A Late Pleistocene (Wisconsinan) avifauna from West Palm Beach, Florida

by Jonathan J. Becker

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The West Palm Beach local fauna was collected in 1969 from the western half of tract 17, block 1, plot 9 of Palm Beach Farms, Section 28, Township 43 S., Range 42 E., Palm Beach County, Florida (26°42'N, 80°10'W). Converse (1973) described the excavation of this locality and gave a preliminary faunal list of fish, amphibians, reptiles, and mammals. Radiocarbon dating of a mastodon rib from this site produced a date of 21,150 ± 400 years Before Present (Buckley & Willis 1972), which places it near the time of the maximum extent of the Wisconsinan glaciation. This date agrees with the presence of the late Rancholabrean mammalian species *Tapirus veroensis*, *Mammuthus jeffersonii* and *Bison antiquus* from this site.